Mar. Freshwater Res., 1995, **46**, 1127–35

Age and Growth of the Queen Scallop, *Equichlamys bifrons*, in the D'Entrecasteaux Channel and Huon River Estuary, Tasmania

B. M. Wolf and R. W. G. White

Fish Research Group, Department of Zoology, University of Tasmania, GPO Box 252C, Hobart, Tas. 7001, Australia.

Abstract. Growth of the queen scallop, *Equichlamys bifrons*, was examined at one site in the D'Entrecasteaux Channel and two sites in the Huon River estuary (Tasmania) by analysing growth rings on the shell and shell hinge ligament, tagging scallops, and using size–frequency techniques. Regular sampling of scallops revealed that shell growth of *E. bifrons* is seasonal, commencing in late spring and stopping in late autumn. During the remainder of the year, when the water temperature is below ~13°C, shell growth slows or stops and growth rings are formed on the shell and shell hinge ligament. The growth rings on the shell and hinge ligament of *E. bifrons* were verified as being annual by studying the growth of marked scallops. Long-term growth patterns were similar for *E. bifrons* from Middleton (D'Entrecasteaux Channel) and from Deep Bay (Huon River estuary). Tagging data collected over the 1992–93 growing season indicated short-term variation in growth between sites. Size–frequency distributions from Middleton and Deep Bay could not be interpreted because smaller scallops were scarce. Smaller size classes were present at Eggs and Bacon Bay (Huon River estuary) and the size–frequency distribution was resolved into age classes. Reasonable agreement was found between the von Bertalanffy growth parameters obtained from the size frequency, tagging, and growth ring data.

Introduction

Equichlamys bifrons (queen scallop) is a large scallop (150 mm widest diameter) found in New South Wales, Victoria, South Australia and Tasmania (MacPherson and Gabriel 1962). In the D'Entrecasteaux Channel, Tasmania, *E. bifrons* occurs with the doughboy scallop (*Chlamys asperrimus*) and the commercial scallop (*Pecten fumatus*), and all three species have been fished intermittently since about 1915; this was the first scallop fishery in Australia (Gwyther *et al.* 1991) and was the centre of the Australian scallop industry until 1963 (Gwyther 1988). Although the fishery was based principally on *P. fumatus* stocks, this species has not been fished in the channel since 1969. Between 1970 and 1992 the fishery relied on stocks of *E. bifrons* and *C. asperrimus*. The fishery was closed in 1993, mainly owing to the low numbers of these two species (W. Zacharin, personal communication). Despite recurrent collapses in production in this fishery, only the biology of *P. fumatus* has been studied in any detail (Fairbridge 1953; Olsen 1955; Harrison 1961).

The determination of growth in commercially harvested species of scallops is well documented in the literature owing to the importance of this information in fisheries management and aquaculture. Growth in scallops is influenced by the interaction of environmental factors, particularly water temperature and food supply (Broom and Mason 1978), which often results in a seasonal variation in growth. Growth of scallops may also be influenced by reproductive events (Fairbridge 1953), water depth (Mason 1957; Haynes and Hitz 1971; MacDonald and Thompson 1985), food limitation associated with high scallop densities (Gruffydd 1974; Gwyther and McShane 1988), and current flow (Fairbridge 1953).

Growth of scallops is commonly described in terms of an increase in shell height, which is the maximum distance between the dorsal (hinge) and ventral margins. Shell height information is then related to age in order to construct growth curves, which are often fitted to growth models, e.g. von Bertalanffy model, for predictive and comparative purposes. Age and growth rate information in scallops can be obtained by the analysis of growth rings and size–frequency distributions, or from mark and recapture experiments.

The shells of scallops generally have checks or rings separating areas of uninterrupted growth. Ring formation has been linked with cessation of growth due to annual variation of environmental conditions (Stevenson and Dickie 1954; Haynes and Hitz 1971), periods of reproduction (Taylor and Venn 1978), and shock or disturbance (Mason 1957; Merrill *et al.* 1966). Similar but usually more prominent rings (Merrill *et al.* 1966) often occur on the shell hinge ligament (MacDonald and Bourne 1989). The nature of the rings on the shell and hinge ligament must be investigated before they can be used for age and growth studies.

The aims of this study were to compare the growth and age structure of *E. bifrons* at contrasting sites and to compare the results obtained by recording growth rings, analysing size frequencies, and tagging.

1323-1650/95/081127$05.00

Materials and Methods

Study Sites

Equichlamys bifrons was studied at one site in the D'Entrecasteaux Channel and two sites in the Huon River estuary (Fig. 1). The northern extremity of the D'Entrecasteaux Channel lies ~20 km south of Hobart and the channel runs south for ~45 km. The scallop beds at Middleton occur at a depth of 14 m, on a bottom of coarse sand and broken shell. Strong tidal currents (0·5–1·0 m s^{-1}) flow along the north–south axis.

In Eggs and Bacon Bay and Deep Bay, *E. bifrons* is found at depths of between 2 and 4 m, on a silty bottom scattered throughout the seagrasses *Heterozostera tasmanica* and *Halophila australis*. These sites are sheltered and subject to only weak currents.

Bottom water temperature was recorded regularly at each site by divers using a hand-held thermometer (Fig. 2).

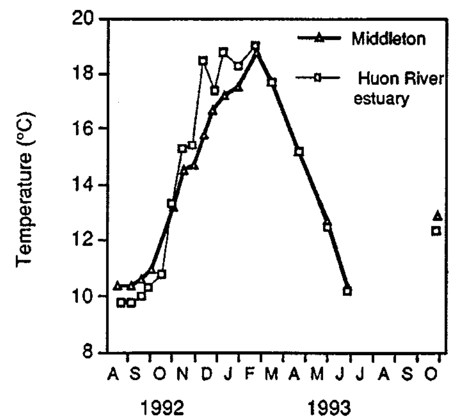

Fig. 2. Seasonal variation in the bottom water temperature at Middleton and the Huon River estuary sites (Eggs and Bacon Bay, August and September 1992; Deep Bay, October 1992 onwards).

Analysis of Shell and Ligament Rings

Samples of *E. bifrons* were collected by SCUBA divers fortnightly between August 1992 and January 1993 and monthly between February and August 1993. Approximately 30 scallops of a wide size range were collected in each sample from Middleton. Initially, scallops were also taken from Eggs and Bacon Bay, but numbers quickly became depleted in some size classes and the Huon River estuary sampling was switched to Deep Bay in mid October 1992. Shell margins were examined for new growth or the formation of growth rings. The upper (left) valve of *E. bifrons* is larger than and clasps the lower valve, so measurements of shell height to the nearest 0·1 mm were taken from the upper valve with the aid of Vernier calipers. The scallops were shucked and shells stored for later analysis of growth rings.

Growth rings were counted on 102 scallops from Middleton and 109 from Deep Bay. The lower valves were used because the growth rings on the upper valve are often hidden by fouling organisms. A regression equation describing the relationship between the lower and upper valves was determined by measuring both valve heights from 50 scallops over the full size range. The shell height at the formation of each ring was measured with Vernier calipers. The height of each ring on the lower valve was converted to a corresponding upper shell height by using the regression equation. Mean values for the height of each ring were calculated.

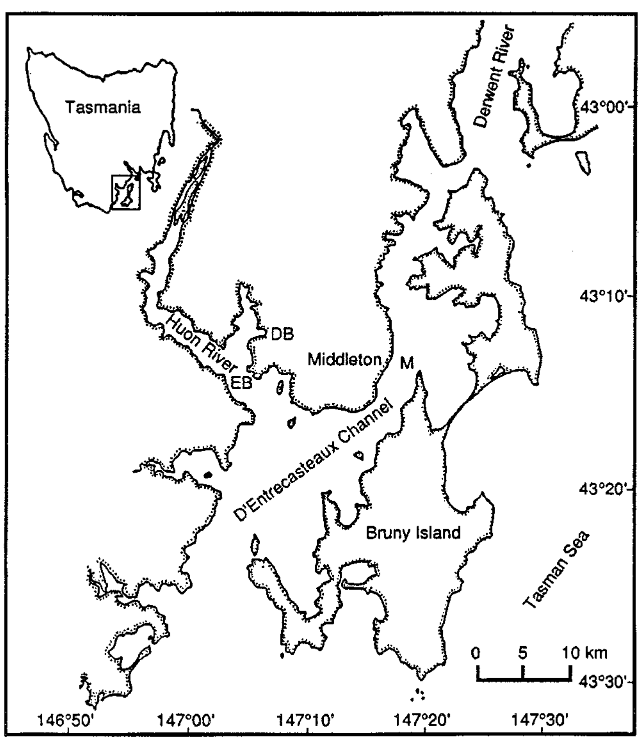

Fig. 1. D'Entrecasteaux Channel and Huon River estuary, showing sampling sites. M, Middleton; EB, Eggs and Bacon Bay; DB, Deep Bay.

Two methods for rapid examination of the ligament growth rings were used. The separation of the upper and lower valves normally resulted in the split of the ligament into two halves. When fresh, each half could be gently picked away from the shell, revealing a ligament scar from which the growth rings could be read. Alternatively, each half of the split ligament was left to dry in place for a few days and then picked out of the socket along with the ligament scar and attached calcareous plate. The growth rings on the calcareous plate were counted under a low-power microscope. This second method was also used by Merrill *et al.* (1966).

To examine the relationship between growth rings on the shell and those on the shell ligament, 100 scallops over the full size range that had been aged from the shells were, on a separate occasion, aged by counting the growth rings on the calcareous plate of the hinge ligament.

Tagging

Scallops were tagged at Middleton (n = 373), Deep Bay (89) and Eggs and Bacon Bay (64) in September and October 1992. Scallops of all sizes were collected by SCUBA divers, taken to the surface, and placed immediately into large bins containing sea water. Serially numbered Hallprint flexible plastic tags (4 × 9 mm) were attached with cyanoacrylate adhesive to the lower valve. Shell heights were measured to the nearest 0·1 mm with Vernier calipers. Scallops were returned by divers within 2 h of capture near to the place from where they were collected.

Periodically, 15–40 tagged scallops were remeasured *in situ* and replaced. They were handled a maximum of four times between tagging and final recapture and were taken to the laboratory for final measurements of shell height in late October 1993, ~400 days after tagging.

Size Frequency

Between August and November 1992, when growth rings were forming, divers collected 525 scallops from Middleton, 181 from Deep Bay, and 226 from Eggs and Bacon Bay. These scallops were used for shell height–frequency analysis in an attempt to identify size classes. The MIX program (Macdonald and Green 1988) was used to analyse the size–frequency distribution data. The program fits a series of normal curves to a multimodal size–frequency distribution. By a series of iterative calculations, it estimates the mean and standard deviation of each component distribution and the proportion of the sample represented by each component curve. The means were constrained to lie along a von Bertalanffy growth curve, and the usual growth curve parameters (L_∞ and K) were calculated by the program.

Growth Models

The von Bertalanffy growth model (von Bertalanffy 1938) was fitted to the data for shell height at ring formation and to tag–recapture data and size–frequency data; the equation used was a form suitable for results from tagging experiments (Fabens 1965) in which size at tagging, size at recovery, and time intervals are known:

$$L_{t+1} - L_t = (L_\infty - L_t)(1 - e^{-Kt}),$$

where L_∞ is asymptotic shell height, L_t is initial shell height, L_{t+1} is final shell height, t is the time interval between the initial and final shell height measurements, and K is the growth coefficient. The von Bertalanffy growth curve was fitted by non-linear least-squares regression using iterative computation on the SYSTAT 5.2 statistics package on an Apple Macintosh computer. K and L_∞ were estimated by this technique. Growth curves were plotted under the assumption that *E. bifrons* has zero shell height at time zero.

The Walford plot (Walford 1946) was also used to describe the growth of tagged scallops. The shell height at the time of final recapture was plotted against the shell height at the time of marking. The Walford line was fitted by least-squares regression. The natural logarithm of the Walford slope provides an estimate of the growth coefficient (K), and an estimate of the asymptotic shell height (L_∞) is taken as the point where the Walford line indicates $L_{t+1} = L_t$. The von Bertalanffy growth parameters were estimated from the Walford line and growth curves were constructed.

Results

Seasonality of Shell Growth

No shell growth was observed at Deep Bay or Middleton from August 1992 until 24 and 27 November 1992 respectively. The recommencement of growth could be seen when new shell emerged from beneath the older shell. The older shell margin was then distinguished as a prominent growth ring by the crowding of shell striae in this region and well spaced striae of the emerging lighter coloured shell. The crowding of shell striae following the period of rapid shell growth was apparent in a sample taken from Middleton on 28 May 1993. This suggested that growth ring formation occurred over the winter and spring period (i.e. late May to late November).

Analysis of Shell and Ligament Rings

The regression of the upper valve (y) on the lower valve (x) gave the equation

$$y = 1{\cdot}055x - 1{\cdot}492\ (r = 1{\cdot}00,\ \text{d.f.} = 48,\ P < 0{\cdot}0001).$$

This relationship holds to a lower shell height of ~30 mm. Below this, the shell height of the right valve equals that of the left valve. The analysis of the shell growth rings indicated 12 year classes. Scallops were found with 2–13 growth rings. The mean shell heights at every ring formation for each year class are presented in Table 1. The first growth ring on the older scallops could not always be detected because the umbonal region of some shells was badly worn. The rings on older scallops also were very crowded towards the shell margin and were difficult to detect and measure. These animals were used only if the ring count on the shell was confirmed by a count of the rings on the ligament. Scallops with up to 13 growth rings occurred at Middleton; none with more than 10 rings were found at Deep Bay.

The ageing of the scallops from the shell growth rings was compared against that from the calcareous plate of the hinge ligament. From 100 scallops, eight were aged differently by the two techniques. Differences in the number of growth rings between techniques were never greater than one and were found only in scallops with eight or more growth rings. Differences were both positive and negative.

The growth curves in Fig. 3 are plotted from the mean shell heights at each ring formation for the shells that were studied at Middleton and Deep Bay. These curves are composite growth curves representing a combination of growth for many different years. Growth rates were similar between Middleton and Deep Bay over long time periods.

Knowing the age of the scallops at the deposition of the first growth ring would allow growth ring data to be converted directly into ages. Major spawning occurs in January (Wolf 1993). Formation of the growth ring in this study began in late May, when the young scallops were ~5 months old. The age in years at the time of ring formation is therefore the number of rings less ~7 months.

The von Bertalanffy growth model was fitted to the data on shell height at ring formation. The mean shell growth ring data were converted from ring number to age in years by subtracting 7 months from the ring number. The resultant growth curves, along with the fitted von Bertalanffy growth curves, are compared in Figs 4*a* and 4*b* for Middleton and

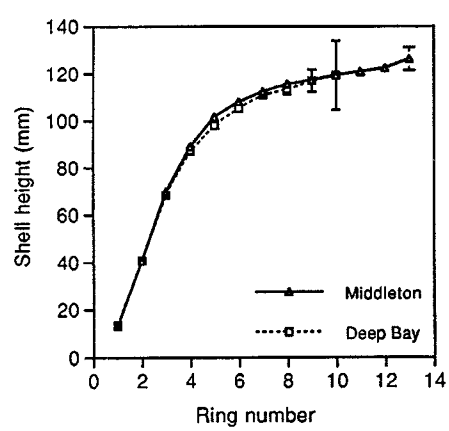

Fig. 3. Mean shell height at ring formation in *Equichlamys bifrons* from Middleton and Deep Bay. Vertical bars, 95% confidence intervals.

Table 1. Mean shell height at ring formation by cohort for *Equichlamys bifrons* from *(a)* Middleton and *(b)* Deep Bay
Mean, raw mean of all measurements

(a) Middleton

Ring no.	1990	1989	1988	1987	1986	1985	1984	1983	1982	1981	1980	1979	*n*	Mean
1	12·6	11·7	13·1	13·5	7·6		–	–	–	–	–	–	27	12·9
2	42·7	40·4	42·1	40·6	36·9		36·3	32·9	40·4	44·1	40·8	40·6	102	40·7
3		72·7	70·6	69·3	63·8		67·9	64·2	68·8	69·7	69·7	73·4	99	69·7
4			90·8	88·6	84·2		84·2	83·8	92·5	86·2	88·4	90·5	93	88·9
5				102·1	99·5		93·8	98·0	101·1	98·3	100·4	101·4	75	101·6
6					110·8		102·7	104·1	107·8	106·4	108·4	109·3	19	108·0
7							108·5	110·1	111·7	111·2	112·7	114·0	17	112·3
8							113·8	111·5	115·4	114·1	115·6	116·9	17	115·5
9								113·5	117·8	115·4	117·1	118·8	14	117·2
10									119·6	118·5	118·7	120·5	13	119·2
11										119·9	120·0	122·8	11	120·7
12											121·5	124·1	10	122·3
13												126·1	3	126·1
No. in year class	3	6	19	55	2	0	3	1	2	1	7	3		

(b) Deep Bay

Ring no.	1990	1989	1988	1987	1986	1985	1984	1983	1982	1981	1980	1979	*n*	Mean
1		14·5	12·7	12·7	22·7	10·4	10·0	–	10·8				45	13·5
2		50·6	43·2	37·6	50·0	39·0	39·4	37·8	43·2				109	40·8
3		78·8	71·4	65·6	72·5	65·9	66·7	69·2	66·2				109	68·4
4			90·9	85·1	88·5	84·4	83·7	84·9	82·2				106	87·0
5				99·1	100·0	97·7	95·0	95·3	94·3				69	98·1
6					109·0	106·1	103·4	103·6	101·7				27	105·2
7						113·7	109·6	110·5	109·2				20	110·9
8							113·5	116·1	113·6				10	113·3
9								119·1	116·6				4	116·9
10									119·1				2	119·1
No. in year class	0	3	38	41	7	10	6	2	2	0	0	0		

Deep Bay respectively. The von Bertalanffy model provided good representation of the growth ring data at both sites. The von Bertalanffy parameter K was estimated to be 0·373 at Middleton and 0·331 at Deep Bay. L_∞ was estimated at 128·25 mm for Middleton and 132·70 mm for Deep Bay.

Tagging

Scallops with shell heights ranging from 31·3 to 126·1 mm were tagged. In late October 1993, 148 (40%) tagged scallops were recovered alive from Middleton, 50 (56%) from Deep Bay, and 11 (17%) from Eggs and Bacon Bay. During the period of liberty, 20 (5%), 1 (1%), and 10 (16%) of the tagged scallops were recovered dead from Middleton, Deep Bay, and Eggs and Bacon Bay respectively.

The influence of increased handling (i.e. intermediate measurements of shell height by divers) on the growth rates of tagged Middleton scallops was investigated by analysis of covariance (ANCOVA), with shell height at tagging as a cofactor. Increased handling of the scallops did not significantly influence growth rates (ANCOVA: $P = 0{\cdot}42$) (Table 2). The different handling categories were therefore pooled for each site. A comparison of tagged scallop growth rates between the three sites, with shell height at tagging as a cofactor, revealed significant inter-site differences (ANCOVA: $P < 0{\cdot}001$) (Table 3). The growth rate of Middleton scallops during the tagging period was significantly greater than that of Deep Bay scallops (Tukey's test: $P < 0{\cdot}05$) and Eggs and Bacon Bay scallops (Tukey's test: $P < 0{\cdot}05$). The growth rate of tagged scallops was also

Table 2. Analysis of covariance of growth rates of tagged *Equichlamys bifrons* from Middleton with different handling regimes
Cofactor is shell height at tagging

Source	Sum of squares	Degrees of freedom	Mean square	*F*-ratio	*P*
Handling	20·685	3	6·895	0·940	0·424
Shell height	1504·506	1	1504·506	205·015	<0·001
Error	961·345	131	7·338		

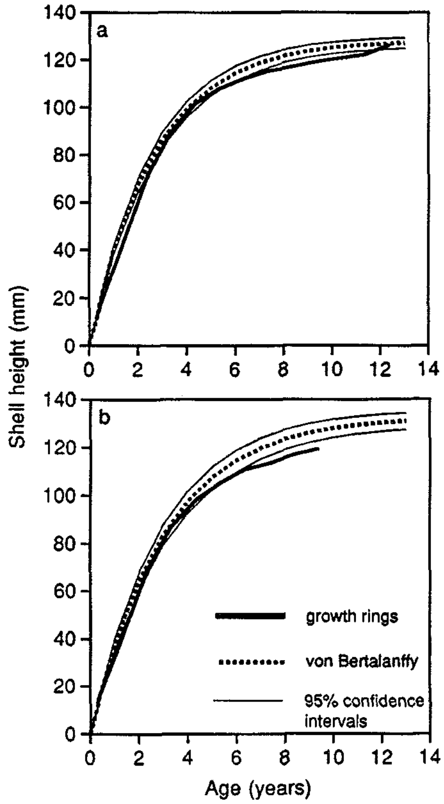

Fig. 4. von Bertalanffy growth curves fitted to shell growth ring data and compared with mean shell height at ring formation (adjusted to age) for *Equichlamys bifrons* from *(a)* Middleton and *(b)* Deep Bay.

greater at Deep Bay than at Eggs and Bacon Bay (Tukey's test: $P < 0{\cdot}05$).

The pooled tagging data from each site for scallops that had been at liberty for one growing season was used for the construction of Walford plots. The equations for the fit of the Walford line were

$$y = 0{\cdot}610x + 49{\cdot}222\ (r = 0{\cdot}973,\ \text{d.f.} = 146,\ P < 0{\cdot}001),$$
$$y = 0{\cdot}701x + 38{\cdot}737\ (r = 0{\cdot}943,\ \text{d.f.} = 48,\ P < 0{\cdot}001),\ \text{and}$$
$$y = 0{\cdot}607x + 43{\cdot}769\ (r = 0{\cdot}973,\ \text{d.f.} = 9,\ P < 0{\cdot}001)$$

for Middleton, Deep Bay, and Eggs and Bacon Bay respectively. From the Walford plot for Middleton, K and L_∞ were estimated as 0·494 and 126·21 mm respectively. For Deep Bay, K and L_∞ were 0·355 and 129·55 mm. The Walford plot for Eggs and Bacon Bay gave a K value of 0·499 and an L_∞ value of 111·37 mm.

The von Bertalanffy model was fitted to the pooled tagging data from each site (Figs 5*a*, 5*b* and 5*c* for Middleton, Deep Bay, and Eggs and Bacon Bay respectively). From this model, K and L_∞ were respectively estimated to be 0·445 and 126·74 mm at Middleton, 0·332 and 129·76 mm at Deep Bay, and 0·461 and 111·24 mm at Eggs and Bacon Bay. The von Bertalanffy growth curves from each site are compared in Fig. 6 and illustrate the inter-site growth differences of tagged animals as found by ANCOVA.

Table 3. Analysis of covariance of growth rates of tagged *Equichlamys bifrons* from Middleton, Deep Bay, and Eggs and Bacon Bay
Cofactor is shell height at tagging

Source	Sum of squares	Degrees of freedom	Mean square	*F*-ratio	*P*
Site	220·709	2	110·354	16·328	<0·001
Shell height	3565·298	1	3565·298	527·533	<0·001
Error	1385·479	205	6·758		

Size Frequency

The size–frequency data from Middleton and Deep Bay could not be resolved into modal size classes with the MIX program. This was due to the poor representation of smaller size classes at these sites and the difficulty of analysing the extensive overlap of the larger size classes. Smaller size classes were well represented at Eggs and Bacon Bay and clear size modes were identified. In the MIX analysis, the means of each component were constrained to lie along a von Bertalanffy growth curve and the older age classes were merged. From this, K and L_∞ were respectively estimated to be 0·381 and 126·44 mm. χ^2 analysis indicated that the fitted model was not significantly different from the data ($\chi^2 = 49{\cdot}54$, d.f. = 44, $P = 0{\cdot}2617$).

Comparison of Growth Measurements

The values of K and L_∞ estimated from the different techniques are summarized in Table 4. The growth curves from each of these methods are compared in Fig. 7. For Middleton and Deep Bay scallops, the three growth curve

Table 4. L_∞ and K values for *Equichlamys bifrons* from the three sites, derived from different data sources and methods of analysis

Data source	Analysis	Site	L_∞	K
Shell growth rings	von Bertalanffy	Middleton	128.25	0.373
Shell growth rings	von Bertalanffy	Deep Bay	132.70	0.331
Tagging	von Bertalanffy	Middleton	126.74	0.445
Tagging	von Bertalanffy	Deep Bay	129.76	0.332
Tagging	von Bertalanffy	Eggs and Bacon Bay	111.24	0.461
Tagging	Walford plot	Middleton	126.21	0.494
Tagging	Walford plot	Deep Bay	129.55	0.355
Tagging	Walford plot	Eggs and Bacon Bay	111.37	0.499
Length–frequency	von Bertalanffy	Eggs and Bacon Bay	126.44	0.381

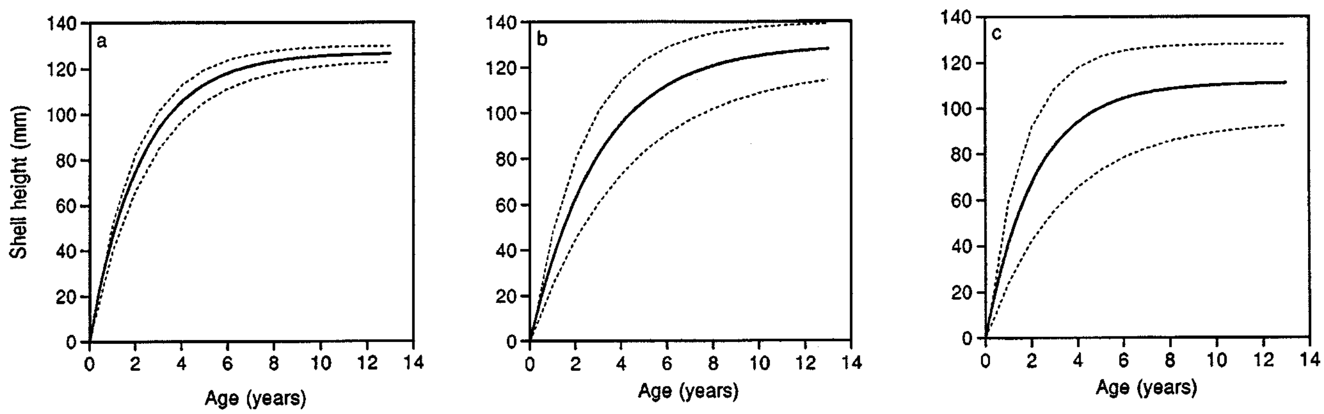

Fig. 5. von Bertalanffy growth curves fitted to *Equichlamys bifrons* tag returns from *(a)* Middleton, *(b)* Deep Bay, and *(c)* Eggs and Bacon Bay. Dashed lines, 95% confidence intervals.

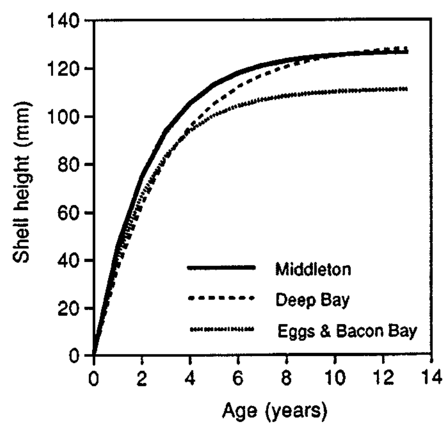

Fig. 6. Growth curves of *Equichlamys bifrons* at Middleton, Deep Bay, and Eggs and Bacon Bay, derived from von Bertalanffy analysis of tagged scallops.

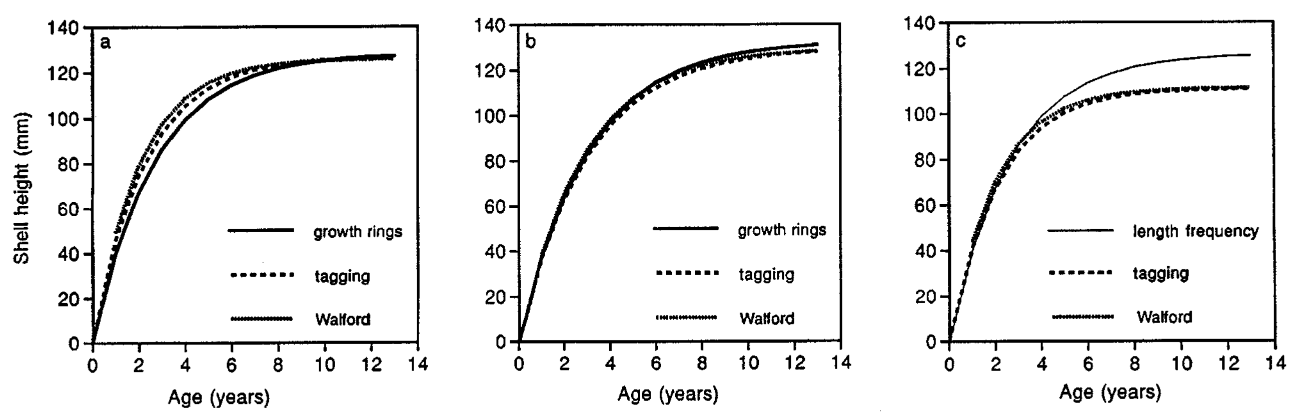

Fig. 7. Growth curves for *Equichlamys bifrons* from *(a)* Middleton and *(b)* Deep Bay, derived from shell growth rings (von Bertalanffy) and tagging data (von Bertalanffy and Walford plot), and *(c)* Eggs and Bacon Bay, derived from length–frequency analysis (von Bertalanffy) and tagging data (von Bertalanffy and Walford plot).

derivations were very similar within each site. For scallops from Eggs and Bacon Bay, the von Bertalanffy and Walford curves corresponded closely but differed from the growth curve derived from the size–frequency data above a shell height of ~90 mm. This difference may be the result of the low number (11) of tag returns upon which the von Bertalanffy and Walford curves are based.

Discussion

Regular sampling of *Equichlamys bifrons* and examination of the shell margins over a 12-month period indicated that growth ring formation occurred annually. Growth rings on the ligament correspond with those on the shell. Further support for the annual nature of the growth rings was provided by comparing the growth curves derived from growth rings with those derived from tagging studies independent of growth ring counts. These growth curves from Deep Bay were almost identical. The curves from Middleton were similar, especially given that the growth curves derived from the growth rings represented the growth of scallops back to 1979, whereas the growth curves from the tagging represented only one year of growth in 1992–93.

Scallop species with annual growth rings are typically from temperate waters and include *Pecten fumatus*, *P. maximus*, *Placopecten magellanicus*, *Patinopecten caurinus*, *Chlamys varia* and *C. opercularis*. In some species, there may be no growth ring in the first year (Conan and Shafee 1978) or the first annual ring may be faint (Richardson *et al.* 1982). The first growth ring of *E. bifrons* is not as distinct as subsequent rings because it is deposited at a shell height of ~13 mm. In older individuals in which the umbonal region of the shell is worn, the detection of the first ring is very difficult.

Low water temperatures in winter are most frequently linked with growth ring formation in scallops. In *Placopecten magellanicus*, formation of the shell annuli has been closely linked with low winter temperature, as the growth rings in scallops from shallow water, where effects of winter are more severe, are more pronounced than those in scallops from deeper waters, where water temperatures vary less (Merrill *et al.* 1966). Similarly, the growth rings in *Patinopecten caurinus* are formed in winter (Haynes and Hitz 1971), and the cessation of growth in *Chlamys varia* is related to low-temperature conditions (Conan and Shafee 1978). In *C. opercularis* (Broom and Mason 1978; Taylor and Venn 1978) and *Pecten maximus* (Mason 1957), growth ring formation is related to both low temperatures and scarcity of food. In the present study, growth ring formation in *E. bifrons* occurred over the winter–spring period when water temperatures were below ~13°C. In the absence of data on food conditions at any of the sites during this work, it is difficult to predict the confounding effects of food and temperature on the patterns of shell growth in *E. bifrons*.

Sub-annual or supernumerary growth marks occur in most scallop species, including *Pecten fumatus* (Fairbridge 1953), *Placopecten magellanicus* (Stevenson and Dickie 1954; Merrill *et al.* 1966), *Pecten maximus* (Mason 1957), *Chlamys varia* (Conan and Shafee 1978), and *C. opercularis* (Broom and Mason 1978; Taylor and Venn 1978). Disturbance checks were often found on the shell of *E. bifrons* but were easily identified by their jagged nature and irregular spacing compared with annual rings. Shells with disturbance marks were not used for age determinations in this study because they provided a possible source of error.

The formation of disturbance checks is often associated with handling from measuring or tagging scallops (Mason 1957; Merrill *et al.* 1966; Taylor and Venn 1978). The scallops in this study were tagged during the period of growth ring formation by a marking method that minimized the stress placed on the scallop (Heald 1978), consequently a disturbance check was not evident. Some tagged scallops in this study were measured by divers at intervals between the initial and final measuring dates. No additional checks associated with intermediate measurement dates were observed on the shells. Growth rates were not significantly different between scallops that had received different degrees of handling. Similarly, growth rates of *Chlamys opercularis* held in suspended cages are not influenced by increased handling associated with measuring growth (Richardson *et al.* 1982).

The von Bertalanffy model has been applied regularly to shell growth in scallops (e.g. Conan and Shafee 1978; Taylor and Venn 1978; MacDonald and Bourne 1987). The von Bertalanffy growth equation adequately described growth in *Equichlamys bifrons*. The form of the equation used in the present study does not, however, allow for seasonal growth when applied to growth data from tagged animals. The recaptured tagged scallops were at liberty for periods close to one year, so seasonal influences on the growth parameters were minimal. Heald and Caputi (1981) recognized seasonal differences in the growth parameters derived from tagging studies on *Amusium balloti*. They overcame this by providing estimates of the von Bertalanffy parameters for both the summer and winter growth periods. Pauly *et al.* (1992) proposed a modified version of the von Bertalanffy growth function in which a sine wave was incorporated to account for seasonal fluctuations in the growth of fishes. Similarly, Shafee and Lucas (1980) used instantaneous growth rate to overcome problems associated with discontinuous growth in *Chlamys varia*. In the present study, the data were not suitable for determination of instantaneous growth rate or application of the model developed by Pauly *et al.* (1992) because tagged scallops were not measured sufficiently frequently.

Smaller size classes of *E. bifrons* were poorly represented at Middleton and Deep Bay, and in the larger size classes the annual growth increments were not sufficient to show any clear progression of modal size classes in the size–frequency data. The Middleton and Deep Bay size–frequency data therefore could not be resolved. The dominance of the 1987 and 1988 cohorts at Middleton and Deep Bay was indicative of the variable recruitment that is prevalent in most scallop fisheries. Fairbridge (1953), in his studies on *Pecten fumatus* in the D'Entrecasteaux Channel, could not identify any age groups owing to the lack of smaller size classes and dominance by larger size classes. Similarly, the age of *Placopecten magellanicus* (Stevenson and Dickie 1954), *Patinopecten caurinus* (Haynes and Hitz 1971), and *Chlamys opercularis* (Taylor and Venn 1978) can be reliably identified only from size–frequency distributions in which separate modes of the smaller scallops are present. In this study, the presence of smaller, segregated, size classes at Eggs and Bacon Bay allowed the von Bertalanffy growth parameters to be estimated. There was reasonable agreement between the growth curves derived from the size–frequency analysis and the tagging data at Eggs and Bacon Bay, considering the low number of tag returns from this site.

The growth curves derived from the interpretation of growth rings on the shell of *E. bifrons* were very similar at Middleton and Deep Bay. These curves were derived from animals that were spawned between 1979 and 1990. They represent the growth of about 12 cohorts and demonstrate the long-term similarity in growth patterns between Middleton and Deep Bay scallops. This suggests that the environmental variables important for growth in *E. bifrons* are likely to be similar between Middleton and Deep Bay over long time periods.

The analysis of tagging data, however, revealed that the growth rates of *E. bifrons* were significantly greater at Middleton than at Deep Bay for the 1992–93 growing season. When growth curves derived from tagging and growth rings were compared, there was evidence to suggest that growth conditions at Middleton during 1992–93 were more favourable than in past years. At Deep Bay the growth curves from tagging and shell rings were very similar, suggesting that growth conditions at this site were comparable to those of past years. No long-term data on temperature or food are available for the sample sites; it is likely, however, that local differences in one or both of these variables may have resulted in different growth rates during 1992–93.

Annual variations in growth rates of scallops have been documented in the literature. Unusually high water temperatures during El Niño conditions resulted in better than usual growth in *Argopecten purpuratus* near Pisco, Peru (Wolff 1987). *Pecten fumatus* in Port Phillip Bay grows much faster now than it did before it was first commercially exploited in 1963, probably as a result of reduced densities leading to less competition for food (Gwyther and McShane 1988). Similarly, an increase over time in the growth rates of *Pecten maximus* in the Firth of Clyde has been related to lower densities of *Chlamys opercularis* occurring on the scallop beds, suggesting that the earlier growth of *P. maximus* was limited by *C. opercularis* competing for food and space (Mason 1983).

The present study has shown that growth in *E. bifrons* is highly seasonal in the D'Entrecasteaux Channel area, which represents the southern limit of the known distribution of *E. bifrons*. Shell growth occurred only between late November 1992 and late May 1993; only at this time were temperatures higher than ~13°C. Spawning also was initiated during times of peak summer water temperature (Wolf 1993). Investigations of northern populations of *E. bifrons* would provide useful information on the influence of water temperature on the pattern of shell growth and spawning times.

Acknowledgments

Financial assistance and advice was provided by Jeff Whayman, Channel Scallop Farming Enterprises Pty Ltd. We acknowledge the assistance, advice and helpful discussion provided by Will Zacharin, Tasmanian Department of Primary Industry and Fisheries. Divers who helped with this project included Nadine Johnston, Dave Andrews, Colin Shepherd, Gray Coleman, Sue Marsh, Melissa Lorkin, Phil Shelverton and Andrew Poole. Technical assistance was provided by Richard Holmes, Sam Thalmann, Ron Mawbey, Andrew McPhee, Justin Wolf, James Wolf and Henry Wolf. Dr Leon Barmuta provided statistical advice.

References

Bertalanffy, L. von (1938). A quantitative theory of organic growth. (Inquiries on growth laws II). *Human Biology* **10**, 181–213.

Broom, M. J., and Mason, J. (1978). Growth and spawning in the pectinid *Chlamys opercularis* in relation to temperature and phytoplankton concentration. *Marine Biology (Berlin)* **47**, 277–86.

Conan, G., and Shafee, M. S. (1978). Growth and biannual recruitment of the black scallop, *Chlamys varia* (L.) in Lanveoc area, Bay of Brest. *Journal of Experimental Marine Biology and Ecology* **35**, 59–71.

Fabens, A. J. (1965). Properties and fitting of the von Bertalanffy growth curve. *Growth* **29**, 265–89.

Fairbridge, W. S. (1953). A population study of the Tasmanian 'commercial' scallop *Notovola meridionalis* (Tate) (Lamellibranchiata, Pectinidae). *Australian Journal of Marine and Freshwater Research* **4**, 1–40.

Gruffydd, L. D. (1974). The influence of certain environmental factors on the maximum length of the scallop, *Pecten maximus* L. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* **35**, 300–2.

Gwyther, D. (1988). History of management in the Victorian scallop industry. In 'Proceedings of the Australasian Scallop Workshop'. (Eds M.C.L. Dredge, W.F. Zacharin and L.M. Joll.) pp. 12–20. (Tasmanian Government Printer: Hobart.)

Gwyther, D., and McShane, P. E. (1988). Growth rate and natural mortality of the scallop *Pecten alba* Tate in Port Phillip Bay, Australia and evidence for changes in growth rate after a 20-year period. *Fisheries Research (Amsterdam)* **6**, 347–61.

Gwyther, D., Cropp, D. A., Joll, L. M., and Dredge, M. C. L. (1991). Australia. In 'Scallops: Biology, Ecology and Aquaculture'. (Ed. S. E. Shumway.) pp. 835–51. (Elsevier: New York.)

Harrison, A. J. (1961). Annual reproductive cycles in the Tasmanian commercial scallop *Notovola meridionalis.* B.Sc.(Hons) Thesis, University of Tasmania, Hobart.

Haynes, E. B., and Hitz, C. R. (1971). Age and growth of the giant Pacific sea scallop, *Patinopecten caurinus*, from the Strait of Georgia and outer Washington coast. *Journal of the Fisheries Research Board of Canada* **28**, 1335–41.

Heald, D. (1978). A successful marking method for the saucer scallop *Amusium balloti* (Bernardi). *Australian Journal of Marine and Freshwater Research* **29**, 845–51.

Heald, I., and Caputi, N. (1981). Some aspects of the growth, recruitment and reproduction in the southern saucer scallop, *Amusium balloti* (Bernardi 1861) in Shark Bay, Western Australia. *Western Australian Marine Research Laboratories Fisheries Research Bulletin* **25**, 1–33.

Macdonald, P. D. M., and Green, P. E. J. (1988). 'MIX 2.3: An Interactive Program for Fitting Mixtures of Distributions.' (Ichthus Data Systems: Hamilton, Ontario.)

MacDonald, B. A., and Bourne, N. F. (1987). Growth, reproductive output, and energy partitioning in weathervane scallops, *Patinopecten caurinus*, from British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 152–60.

MacDonald, B. A., and Bourne, N. F. (1989). Growth of the purple-hinge rock scallop *Crassadoma gigantea* Gray 1825 under natural conditions and those associated with suspended culture. *Journal of Shellfish Research* **8**, 179–86.

MacDonald, B. A., and Thompson, R. J. (1985). Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus.* 1. Growth rates of shell and somatic tissue. *Marine Ecology Progress Series* **25**, 279–94.

MacPherson, J. H., and Gabriel, C. J. (1962). 'Marine Molluscs of Victoria.' (Melbourne University Press: Melbourne.)

Mason, J. (1957). The age and growth of the scallop *Pecten maximus* (L.) in Manx waters. *Journal of the Marine Biological Association of the United Kingdom* **36**, 473–92.

Mason, J. (1983). 'Scallop and Queen Fisheries in the British Isles.' (Fishing News Books: Farnham, England.) 143 pp.

Merrill, A. S., Posgay, J. A., and Nichy, F. E. (1966). Annual marks on shell and ligament of sea scallop (*Placopecten magellanicus*). *Fisheries Bulletin (US)* **65**, 299–311.

Olsen, A. M. (1955). Underwater studies of the Tasmanian commercial scallop, *Notovola meridionalis. Australian Journal of Marine and Freshwater Research* **6**, 392–409.

Pauly, D., Soriana-Bartz, M., Moreau, J., and Jarre-Teichmann, A. (1992). A new model accounting for seasonal cessation of growth in fishes. *Australian Journal of Marine and Freshwater Research* **43**, 1151–6.

Richardson, C. A., Taylor, A. C., and Venn, T. J. (1982). Growth of the queen scallop *Chlamys opercularis* in suspended cages in the Firth of Clyde. *Journal of the Marine Biological Association of the United Kingdom* **62**, 157–69.

Shafee, M. S., and Lucas, A. (1980). Applications of some growth models to the black scallop, *Chlamys varia* (L.) from Lanveoc, Bay of Brest. *Journal of Experimental Marine Biology and Ecology* **43**, 237–50.

Stevenson, J. A., and Dickie, L. M. (1954). Annual growth rings and rate of growth of the giant scallop, *Placopecten magellanicus* (Gmelin) in the Digby area of the Bay of Fundy. *Journal of the Fisheries Research Board of Canada* **11**, 660–71.

Taylor, R. C., and Venn, T. J. (1978). Growth of the queen scallop *Chlamys opercularis* from the Clyde Sea area. *Journal of the Marine Biological Association of the United Kingdom* **58**, 687–700.

Walford, L. A. (1946). A new graphic method of describing the growth of animals. *Biological Bulletin (Woods Hole)* **90**, 141–7.

Wolf, B. M. (1993). The growth, reproduction and habitat use of the queen scallop, *Equichlamys bifrons* in the D'Entrecasteaux Channel and Huon River estuary, Tasmania. B.Sc.(Hons) Thesis, University of Tasmania, Hobart.

Wolff, M. (1987). Population dynamics of the Peruvian scallop *Argopecten purpuratus* during the El-Niño phenomenon of 1983. *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 1684–91.

Manuscript received 29 March 1995; revised 17 July; accepted 1 August 1995